HABITUATION OF THE WITHDRAWAL RESPONSE IN NEREID POLYCHAETES

2. RATES OF HABITUATION IN INTACT AND DECEREBRATE WORMS

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Most nereid polychaetes are tubiculous or burrowing worms which come to the ends of their tubes or burrows in order to feed.   When exposed in this way the worms are highly susceptible to attack from a wide variety of predators including fishes (*e.g.*, see Scott, 1901, 1902; Jones, 1954; Rae, 1956) birds (Witherby, Jourdain, Ticehurst and Tucker, 1938–41), and crustaceans (Blegvad, 1914).   It is not surprising, therefore, that the worms have well developed withdrawal responses that are elicited by almost any sudden stimulus.

It is now well established that the worms habituate to repeated, innocuous stimulation (Clark, 1960ab; Evans, 1969).   Habituation of escape responses is usually considered to allow for a compromise between the conflicting needs of the animal: the need to respond and escape from its enemies, on the one hand, and the need to continue with normal activities, such as feeding, on the other (*e.g.*, Nicol, 1950).   Habituation of the withdrawal response almost certainly subserves this function in nereids, because under natural conditions the worms are undoubtedly subjected to stimulation from both innocuous and potentially harmful agents; shadows, for example, may be caused by floating seaweed or by passing clouds but also by predators.

The withdrawal response habituates at different rates according to the nature of the stimulus, and it has been suggested that the rate of habituation is related to the significance of the stimulus in terms of the likelihood of it heralding the approach of a predator (*e.g.*, Clark, 1960b).   It is believed that there is a hierarchy of stimuli of increasing urgency to which the worms habituate less and less rapidly.   Tactile stimuli, for example, are highly significant, because they indicate contact between the predator and its prey, and the serpulid *Hydroides dianthus* habituates more slowly to these stimuli than to shadows, which are less urgent (Yerkes, 1906).   Similarly, the sabellid *Branchioma vesiculosum* habituates to shadows but not at all to tactile stimuli (Nicol, 1950) unless the intensity of the stimulus is controlled, in which case habituation is slow (Krasne, 1965).

The normal background of stimulation experienced by worms also influences their reactivity to stimuli.   Worms either do not react at all, or have poorly developed responses to stimuli which they do not usually experience.   Hargitt (1909) found that specimens of *Hydroides* collected from shallow water, where shadows are normally experienced by the worms, responded to shadows, whereas

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worms collected from deep water, where the light is perpetually dim and shadows are not normally experienced, did not react to them.

In the present account, habituation of the withdrawal response has been compared in three nereids to a variety of stimuli. These worms have been collected from Millport, Scotland, where they are found in entirely different habitats and therefore provide an excellent opportunity for comparing the influence of the normal environmental experience of the worms on their rates of habituation to different stimuli.

The nereids chosen for this study, *N. diversicolor, N. pelagica* and *Platynereis dumerilii*, are all common at Millport. *N. diversicolor* lives in burrows which are basically U-shaped but in some circumstances may consist of ramifying galleries (Dales, 1950; Bogucki, 1954; Harley, 1956). At Millport it has been collected from Kames Bay, which is sheltered but subjected to more wave action than the estuarine mud flats, which are the characteristic habitats of this species. There is a lack of brown algae or other agents likely to cause innocuous shadows at Kames Bay.

N. pelagica is found on rocky shores where there are dense growths of seaweeds such as *Fucus* and *Laminaria,* where it is likely to be subjected to a good deal of innocuous stimulation from shadows and mechanical disturbances. At Millport it has been collected from East Flats and Keppel Pier, which are both typical habitats; it is common under stones and in *Laminaria* holdfasts. *N. pelagica* is usually considered to be the typically "errant" nereid, but I have frequently found individuals in poorly constructed mucus tubes under stones.

P. dumerilii is found in grey mucus tubes attached to decaying seaweed and other solid objects at a depth of about 20 m off Kames Bay, Millport (Clark and Milne, 1955), where it has been collected for the present work. At this depth in the sea there is a considerable reduction in light intensity (Atkins, 1945) so that this species might be expected to react to light stimuli differently from *N. diversicolor* and *N. pelagica.*

The supra-oesophageal ganglion is important in the more elaborate behavioral modifications of which nereids are capable (Evans, 1963ab), but its importance in habituation has never been investigated. As a complementary study, this has been investigated by comparing rates of habituation in intact and decerebrate worms.

METHOD

P. dumerilii, N. diversicolor and *N. pelagica* have been collected at Millport, Scotland and the experiments carried out in the laboratories of the Scottish Marine Biological Association at Millport.

The experimental procedure is basically the same as that described in the first part of this paper (Evans, 1969). It differs only in the manner of recording responses and other minor details.

In the present investigation, responses to stimuli were observed for 30 trials at half minute intervals and recorded in terms of the extent of contraction to each stimulus; two or three individuals were observed simultaneously. After collecting, worms were provided with glass tubes, which they inhabited, and kept in tanks circulating with fresh sea water for 3–14 days. During the experiment

TABLE I

Number of worms used in each experiment

Stimulus		Sudden changes in illumination			Mechanical shocks	Sudden decreases and Mechanical shocks	Anterior tactile	Posterior tactile
Species		Sudden increase	Sudden decrease	Shadows				
		Worms in tubes						
N. diversicolor	intact	11	12	10	22	12	11	12
	decerebrate	10	10	10	12	9	10	9
P. dumerillii	intact	18	11	8	16	11	10	10
	decerebrate	20	24	23	10	11	10	10
N. pelagica	intact	10	10	8	11	13	10	10
	decerebrate	10	10	9	10	10	7	10
		Worms not in tubes						
N. diversicolor	intact	10	10	10	10		10	10
	decerebrate	10	10	10	10		10	10
P. dumerilii	intact	10	10	10	18		10	11
	decerebrate	10	10	10	15		10	10
N. pelagica	intact	13	10	10	13		10	10
	decerebrate	10	10	10	13		10	10

they were maintained at the temperature of the sea water tanks by immersing the dish containing them in a temperature conrolled water bath.

Six different stimuli were used: mechanical shocks, tactile stimuli to the anterior and to the posterior ends, sudden increases in illumination (2 ft-c to 30 ft-c), sudden decreases in illumination (30 ft-c to 2 ft-c) and shadows. Shadows were achieved by passing a piece of hardboard, 24″ × 12″, between the more intense of the two light sources and the worms, in about two seconds, so that it caused a decrease in light intensity from 30 ft-c to about 2 ft-c; tactile stimuli by a blunt seeker; and mechanical shocks by a pendulum, consising of a 200 g brass weight suspended by 20 cm of thread, striking the side of the dish after being released from a distance of about 10 cm from it. At least 7 worms were subjected to each stimulus (Table I).

In the first series of experiments worms remained in the glass tubes they were inhabiting throughout the experiment. But in a second series worms were evicted from their tubes and then tested to a series of stimulations while they were crawling or swimming in the dish containing them.

Decerebration was performed in the manner described by Clark and Evans (1961) except that it was found necessary to cauterize the wounds. MS222 (Sandoz Products) was used as an anesthetic; recovery from this is extremely rapid, but worms were not used until the day after the operation.

Theoretically, there are several ways in which animals can habituate. An animal may, for example, be highly reactive initially but habituate rapidly to the stimulus; alternatively, it may be relatively unreactive at first but then

habituate slowly.   Clearly, a consideration of both the habituation rate and the
frequency of responding gives a much clearer indication of the animal's behavior
towards a series of stimulations than either of these factors alone and, con-
sequently, in the present work, the habituation rates and response frequencies
have been assessed for each worm to each stimulus.

The response frequency has been measured for each individual by calculating
the mean number of responses that occurred during the 30 trials given in each
experiment.   Mean performances to different stimuli have been compared sta-
tistically by using a "t" test.   The mean contractions have also been calculated
to each stimulus.

It is unsatisfactory to measure the habituation rate by using a criterion of habitua-
tion of, say five or ten responseless trials, because responses occur after a period of
unreactivity in some worms but not in others (Evans, 1969).   In order to take
into account both the number of worms responding and the extent of contractions
(*i.e.*, the withdrawal in centimeters), the habituation rate (r) has been computed
for populations of worms from the following formula:

$$r = \frac{T}{15}$$

where T is the trial at which 50 per cent of the total withdrawals, measured by the
extent of contraction, have occurred.   The rate of habituaion is related to the
value of r: small values indicate rapid habituation; values larger than one indicate
that habituation is not occurring at all.

Results

Rates of habituation and response frequencies of intact worms in tubes

Sudden increases in illumination elicit slower withdrawal responses, with longer
latencies, than the other stimuli used.   These all elicit the characteristically rapid
withdrawal responses, which occur to sudden decreases in illumination in *N.
diversicolor* (Evans, 1969).   However the manner in which habituation occurs
is not always the same: initially shadows, sudden decreases in illumination and
mechanical shocks elicit extensive withdrawals, which are almost immediately
replaced by incomplete contractions, whereas the initial extensive withdrawals to
tactile stimuli and sudden increases in illumination are gradually lost with suc-
cessive trials.

A worm's response frequency and the rate at which it habituates to a particular
stimulus are usually related.   Worms which respond infrequently to a stimulus
normally habituate rapidly to it and, conversely, reactive worms usually habituate
slowly.   But this is not always so; *N. pelagica* responds infrequently to anterior
tactile stimuli by withdrawing but habituates relatively slowly to them (Table II).

There is some evidence to support the view that the rate of habituation and
also the reactivity of the worms can be related to the severity or significance of
the stimulus.   Habituation is slower and worms respond more frequently to
stimuli which are most likely to act as token stimuli warning them of the approach
of a predator.   For instance paired stimuli are more likely to be related to the ap-
proach of a predator, and are therefore more significant, than stimuli presented alone,

TABLE II

Response frequencies and rates of habituation of intact and decerebrate worms in tubes

	Stimulus						
	Light on	Light off	Moving shadow	Mechan. shock	Light off and mech. shock	Ant. tactile	Post. tactile
	Response frequencies						
Intact *N. diversicolor*	19.4	5.6	4.7	5.1	14.8	26.2	29.9
Decerebrate *N. diversicolor*	6.0	3.5	2.3	3.4	9.8	26.3	29.0
Intact *P. dumerilii*	0.7	3.2	4.0	1.5	10.2	23.2	30.0
Decerebrate *P. dumerilii*	2.2	1.8	0.9	1.8	6.2	29.6	30.0
Intact *N. pelagica*	8.4	7.2	7.8	4.9	6.3	2.2	18.7
Decerebrate *N. pelagica*	0.9	0.8	2.9	2.6	2.2	6.9	12.0
	Habituation rates						
Intact *N. diversicolor*	0.83	0.13	0.13	0.33	1.00	0.80	0.93
Decerebrate *N. diversicolor*	0.40	0.40	0.73	0.30	0.87	0.87	0.93
Intact *P. dumerilii*	0.07	0.13	0.33	0.07	0.73	0.87	0.93
Decerebrate *P. dumerilii*	0.20	0.13	0.13	0.13	0.40	0.73	0.80
Intact *N. pelagica*	0.67	0.27	0.40	0.20	0.40	0.60	0.60
Decerebrate *N. pelagica*	0.33	0.07	0.33	0.47	0.60	0.40	0.40

because a moving predator necessarily creates a complex of stimuli whereas most innocuous agents do not. Both *P. dumerilii* and *N. diversicolor* react significantly more frequently ($P < 0.01$) (Table II), habituate more slowly (Table II) and contract more extensively (Table III) to the simultaneous presentation of sudden decreases in illumination paired with mechanical shocks than to either stimulus presented alone, although in *N. pelagica* there are no significant differences in performance. Similarly tactile stimuli are considered to be more urgent than sudden decreases in illumination, shadows and mechanical shocks because they indicate contact with the stimulating agent and, except in the case of anterior tactile stimuli to *N. pelagica,* worms habituate more slowly, are more reactive and contract more extensively to them than to these other stimuli (Tables II and III). The behavior of *N. pelagica* towards an anterior tactile stimulus is exceptional; initially it normally withdraws but thereafter it responds only spo-

TABLE III

Mean contractions (cm) to different stimuli

Stimulus		Changes in illumination			Mechanical shocks	Mech. shocks and light off	Tactile stimuli	
Species		Light on	Light off	Shadows			Anterior	Posterior
		Worms in tubes						
N. diversicolor	intact	1.08	0.38	0.41	0.31	0.79	2.03	3.34
	decerebrate	0.31	0.20	0.13	0.26	0.64	3.46	3.89
P. dumerilii	intact	0.06	0.34	0.48	0.23	1.16	2.00	2.77
	decerebrate	0.01	0.21	0.08	0.19	0.68	3.01	4.19
N. pelagica	intact	0.75	0.41	0.51	0.39	0.51	0.25	1.82
	decerebrate	0.07	0.08	0.23	0.19	0.19	0.46	0.97
		Worms not in tubes						
N. diversicolor	intact	0.01	0.02	0.00	0.35		1.53	4.50
	decerebrate	0.00	0.00	0.05	0.05		1.25	2.78
P. dumerilii	intact	0.00	0.01	0.04	0.54		0.77	4.05
	decerebrate	0.01	0.01	0.03	0.08		0.75	4.02
N. pelagica	intact	0.34	0.00	0.00	0.03		0.10	0.87
	decerebrate	0.05	0.02	0.01	0.07		0.38	0.78

radically in this manner; more frequently it responds by attacking the seeker and grasping it with its jaws. *N. diversicolor* and *P. dumerilii* both react by withdrawing to an anterior tactile stimulus in significantly more trials than *N. pelagica* ($P < 0.001$), and contractions are more extensive (Table III). However, like *N. pelagica*, habituation to this stimulus is slow (Table II) and sometimes, late in the habituation process, individuals of both *N. diversicolor* and *P. dumerilii* have been observed to attack the seeker.

The differences in behavior towards anterior tactile stimuli can probably be related to the feeding habits of the worms. *N. diversicolor* and *P. dumerillii* are both primarily herbivorous (Harley 1956; Herpin 1925) and react to anterior tactile stimuli in the same manner as other stimuli which are likely to be associated with predators, that is, by withdrawing. However *N. pelagica* feeds largely on animal food; bivalves, gastropods, crustaceans, bryozoans, sponges and hydroids have all been identified in its diet (Rauschenplat, 1901; Blegvad, 1914; Harley, 1956). Some of this food is presumably taken alive, so that slow habituation is advantageous to the worm, because it means that there is no rapid loss of sensory information that might indicate the presence of prey and, as withdrawal is incompatible with this type of feeding behavior; it is equally important that the withdrawal response is relatively unreactive.

There is no obvious relationship between the response frequencies and rates of habituation of the withdrawal response and the normal background of stimulation experienced by the worms. For example, the rates of habituation and response frequencies cannot be related to the worms' normal experience of wave action. Species normally exposed to waves might be expected to habituate rapidly to

mechanical shocks because this stimulus occurs innocuously with each in-coming and out-going tide but, in fact, *N. diversicolor* and *N. pelagica*, which were col- lected from exposed shores at Millport, are significantly more reactive ($P < 0.05$) and habituate more slowly to this stimulus than *P. dumerilii*, which was collected sub-littorally, where it is not exposed to wave action. Similarly in intact worms there are no clear differences in the response frequencies ($P > 0.05$) or rates of habituation to sudden decreases in illumination and shadows in *N. diversicolor*, collected from a habitat free from agents, such as seaweed, which are likely to cause innocuous shadows, *P. dumerilii*, from a depth of 20 m where there is only dim illumination, and *N. pelagica*, collected from a rocky shore where there are such dense growths of seaweed that animals living there must be continually bombarded by shadows (Table II).

The only light stimulus to which habituation rates and response frequencies differ substantially is a sudden increase in illumination. *P. dumerilii* hardly re- sponds to this stimulus at all; it responds significantly less frequently ($P < 0.01$) than either *N. diversicolor* or *N. pelagica*, whose reactivity is intermediate between that of the other species and significantly different from both of them ($P < 0.01$) (Table II). There are similar relationships between the rates of habituation (Table II) and mean extent of contractions (Table III) to sudden increases in illumination in these worms.

P. dumerilii is the only sub-littoral nereid of the three species studied, and its behavior towards sudden increases in illumination appears to resemble that of other sub-littoral polychaetes, such as *Branchiomma vesiculosum* (Nicol, 1950), *Hydroides dianthus* (Yerkes, 1906) and *Serpula vermicularis* (Hess, 1914), which have well developed shadow reflexes but do not respond at all to sudden increases in illumination. A sudden increase in light intensity cannot be related to the approach of a predator and is probably only caused innocuously by, for example, water currents and the emergence of the sun. It is not, therefore, likely to be a warning stimulus so that failure to respond to it or very rapid habituation is clearly advantageous.

Although the littoral nereids *N. pelagica* and *N. diversicolor* habituate slowly to sudden increases in illumination, responses to this stimulus have already been shown to differ in several respects from responses to sudden decreases in illumina- tion. They are slower, for instance, and have longer stimulus-response latencies (Evans, 1969). This suggests that the stimulus may not be a warning stimulus at all and the responses not predator-escape responses. Indeed Clark (1960b) has already suggested that the response of *N. pelagica* to sudden increases in illumination may enable it to withdraw from sudden increases in sunlight and to avoid the harmful effects of solar irradiation. However an alternative explanation is necessary for *N. diversicolor* because this worm has often been observed to feed in bright summer sunshine. In fact, Harley (1956) found that it feeds more in light than in darkness, and, as far as can be seen, individuals suffer no ill-effects of solar irradiation. A possible explanation of the behavior to sudden increases in illumination is that the stimulus indicates exposure which would occur if the posterior end of the worm is extended from the burrow or if the substratum is disturbed. Withdrawal is important to the exposed worm, because it is sus- ceptible to attack from a predator but, unless it is accompanied by other stimuli,

TABLE IV

Response frequencies and habituation rates of intact and decerebrate worms not in tubes

	Stimulus					
	Light on	Light off	Moving shadow	Mechan. shock	Ant. tactile	Post. tactile
	Response frequencies					
Intact *N. diversicolor*	0.1	0.1	0	2.6	15.1	29.0
Decerebrate *N. diversicolor*	0	0	0.9	0.6	17.5	25.6
Intact *P. dumerilii*	0	0.1	0.3	3.0	10.0	28.8
Decerebrate *P. dumerilii*	0.1	0.2	0.3	0.9	12.8	29.5
Intact *N. pelagica*	5.3	0.1	0	0.3	1.5	9.0
Decerebrate *N. pelagica*	0.8	0.3	0.2	0.8	5.2	10.2
	Habituation rates					
Intact *N. diversicolor*	0.07	0.13	0	0.40	0.40	0.80
Decerebrate *N. diversicolor*	0	0	0.07	0.13	0.73	0.93
Intact *P. dumerilii*	0	0.07	0.20	0.40	0.87	0.93
Decerebrate *P. dumerilii*	0.07	0.07	0.13	0.13	0.53	0.87
Intact *N. pelagica*	0.93	0.07	0	0.07	1.00	0.87
Decerebrate *N. pelagica*	0.13	0.07	0.07	0.13	0.93	0.60

warning of the approach of a predator, the slow withdrawal response which occurs to sudden increases in illumination in the laboratory would be adequate.

Rates of habituation and response frequencies of intact worms not in tubes

Nereids are often considered to be typically "errant" polychaetes, and although this view is unjustified because most species are burrowing or tubiculous animals, there is no doubt that they are capable of crawling and swimming outside their tubes or burrows. The extent to which nereids leave their tubes or burrows is unknown, but *N. diversicolor* has occasionally been seen crawling across mud, and *N. pelagica* is frequently found beneath stones under which there is no evidence of a tube. Many species leave their tubes in order to reproduce, and these include *N. diversicolor* which copulates on the surface mud (references in Clark, 1961), and *P. dumerilii* which swarms at the surface of the sea (Sorby, 1906); the breeding habits of *N. pelagica* do not appear to have been recorded.

Except in the case of responses of *P. dumerilii* to mechanical shocks, worms outside their tubes respond much less frequently to stimuli than worms in tubes (Table IV; *cf.* Table II). Similarly habituation rates are faster in worms outside their tubes, except to sudden increases in illumination and tactile stimuli for *N. pelagica* and mechanical shocks for *N. diversicolor* and *P. dumerilii*. In general, the differences in performance are relatively large to light stimuli and small to tactile stimuli.

The response frequencies and habituation rates of nereids in these experiments can probably be related to the importance of the withdrawal response to worms

outside their tubes or burrows. It can no longer effect escape from predators and in general, therefore, responses to stimuli which might be caused by predators are no longer advantageous, particularly as withdrawal usually inhibits movement. However tactile stimuli may be of significance to worms outside tubes or burrows; withdrawals of the anterior end function as avoiding reactions to solid objects, and posterior end withdrawals to tactile stimuli are usually followed by accelerated movement away from the source of stimulation so that, unlike withdrawals to other stimuli, they may be effective in aiding escape from predators. If this is so it is not surprising that the worms continue to habituate slowly and react frequently to tactile stimuli when they are not confined to tubes.

The effect of decerebration on the rates of habituation and response frequencies

Decerebrate worms react to stimuli in the same manner as intact ones except that irrigating movements are only inhibited while a worm is in the process of contracting; decerebrate worms irrigate incessantly. It is surprising that the worms respond to changes in illumination after removal of the supra-esophageal ganglion because the operation involves removal of the eyes, which are situated immediately dorsal to the ganglion. Light receptors are probably located in the epidermis of the body wall and, in fact, Langdon (1900) identified some spiral organs in the epidermis of *N. virens* as light receptors.

Removal of the supra-esophageal ganglion has apparently little effect on the rates of habituation and response frequencies to different stimuli. Without the ganglion, worms still habituate to repeated stimulations, and similar relationships exist between the rates of habituation and response frequencies to stimuli to those in intact animals (Tables II and IV). For example, both decerebrate and intact worms out of tubes are generally less reactive to anterior and posterior tactile stimuli than worms in tubes.

In most cases decerebrate worms respond less frequently and habituate more rapidly than intact ones, but this can probably be attributed to the effects of the anesthetic and operation, which invariably involves the loss of some blood and coelomic fluid. There are, however, two notable exceptions in which decerebrate worms are either more reactive or habituate more slowly than intact worms. First, decerebrate worms respond more frequently than intact ones to anterior tactile stimuli (Tables II and IV), but, although care was taken not to stimulate the wound, this may be due to increased sensitivity at the anterior end as a result of the operation and, in fact, in most cases these worms habituate more rapidly than intact ones. Secondly, decerebrate *N. diversicolor* in tubes habituate more slowly to shadows and sudden decreases in illumination than intact worms (Table II). However, in this case the decerebrate worms actually responded less frequently than intact worms but habituated in a different manner from them. Decerebrate worms did not contract as extensively to the initial stimulations as intact worms, and therefore the loss of the response was gradual (*i.e.,* slow habituation) whereas intact worms habituated characteristically; there was a sudden loss of the initial extensive contraction (*i.e.,* rapid habituation) (Fig. 1). In fact, both decerebrate and intact worms continued to respond for about the same number of trials to these stimuli.
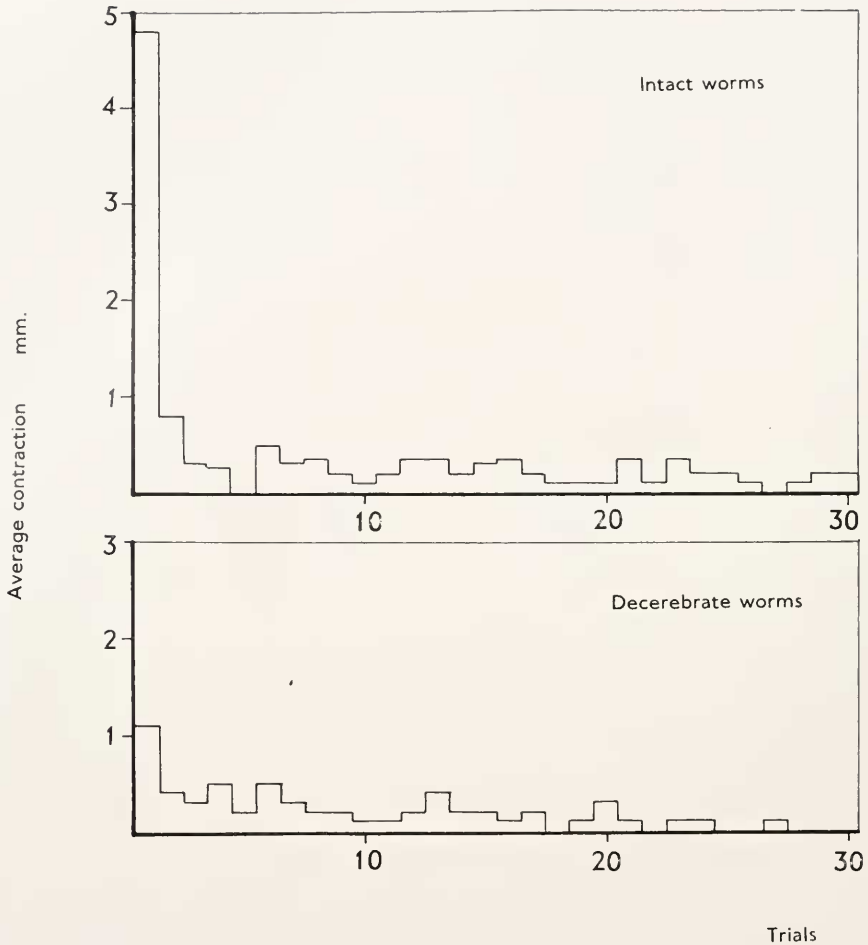
FIGURE 1.   Habituation of 12 intact and 10 decerebrate *N. diversicolor* to sudden decreases in illumination.

DISCUSSION

The process of habituation in *Nereis* is not dependent upon the presence of the supra-oesophageal ganglion.   Withdrawal is still elicited by stimuli in decerebrate worms, and there are similar relationships between the rates of habituation to different stimuli in intact and decerebrate worms.

Habituation has already been demonstrated in both vertebrates and invertebrates deprived of the higher centers of the central nervous system.   For example, spinal rats (Prosser and Hunter, 1936) are capable of habituating.   In the octopus the situation is less clear.   Boycott (1954) has shown that octopuses lacking all of the higher centers but the optic lobes, which are necessary for sight, will habituate to a moving card in the visual field.   Initially the animals withdraw but soon come to ignore the stimulus.   Habituation is occurring in either the optic lobes or the

lower centers of the nervous system. However, in another situation the higher centers are definitely necessary for habituation. Wells (1961) found that, after a few trials, intact octopuses would learn not to respond to an inedible cylinder by taking it to the mouth, but this type of habituation did not usually occur in animals with inferior lobe lesions.

Young (1961) recognizes two types of habituation, apart from the extinction of conditioned responses. First, there is the habituation of inborn avoidance responses and secondly, the loss of exploratory responses to moving objects. In the two invertebrates so far studied, *Nereis* and *Octopus,* higher centers are not apparently necessary for the habituation of avoidance responses, but, as stated above, they are necessary in *Octopus* for habituation of an exploratory response to an inedible cylinder. However, in the latter case the learning may be more complex than the habituation of an avoidance response, because it involves not only the failure of an exploratory response, but the acquisition of a rejectory response; the cylinder is actively rejected by the octopus. The learning may be more similar to associative learning than habituation, and it is interesting that the inferior lobes, which are necessary for the octopus to learn to reject the cylinder, are also the centers of associative tactile learning.

There is little doubt that the reactivity and habituation rate of the withdrawal response in nereids and other polychaetes is related, in at least some ways, to the significance of the stimulus. For example, sudden increases in illumination, which cannot be related to the approach of a predator, never elicit withdrawal in *Branchiomma vesiculosum* (Nicol, 1950) and, although *P. dumerilii* sometimes responds to this stimulus, it habituates to it extremely rapidly. Stimuli which presumably act as token stimuli warning the animals of the approach of a predator are naturally not all of the same significance. There is a hierarchy of stimuli to which the worms are less and less reactive and to which they habituate more and more rapidly which can probably be associated with the likelihood of these stimuli representing predators under natural conditions. Paired stimuli are presumably more significant than the constituent ones presented alone, because moving predators necessarily cause a simultaneous complex of stimuli, and it is now known that *Mercierella enigmatica* (Rullier, 1948), *N. pelagica* (Clark, 1960b) and in the present work, *N. diversicolor* and *P. dumerilii,* habituate more slowly to paired stimuli than single ones. Similarly tactile stimuli are significant, because they indicate contact with the stimulating agent, and worms, such as *Branchiomma vesiculosum* (Nicol, 1950; Krasne, 1965), *Hydroides dianthus* (Yerkes, 1906) and *N. diversicolor* and *P. dumerilii,* habituate extremely slowly to them. *N. pelagica* is an exception in this respect, because it attacks the seeker by grasping it with its jaws more often than it withdraws when stimulaed by it. However, *N. pelagica* is carnivorous so that it seems likely that this behavior can be related to the worm's feeding habits. *P. dumerilii* and *N. diversicolor* are both herbivorous, and, although they have both been observed to attack the seeker occasionally, they only do so after a long series of trials.

The effect of environmental experience on the rates of habituation and reactivity to different stimuli is obscure. *N. diversicolor, N. pelagica* and *P. dumerilii* are found in entirely different ecological situations, but their rates of habituation and response frequencies to stimuli are remarkably similar. However, unless dif-

ferences in this kind of comparison are particularly clear their significance can only be assessed with suspicion. In order to assess the significance of a particular stimulus in different habitats the important consideration is the relative preponderance of that stimulus caused by innocuous and harmful agents in each habitat, and there are probably insuperable difficulties in obtaining such information.

It is not clear from the data whether the rate of habituation to a particular stimulus is innately determined in nereids, and modified only as a result of recent experience, or whether it is adapted to the background of stimulation experienced over a longer period of time. The latter situation is advantageous if individuals of a species are likely to occur in different habitats in which selective pressures vary to such an extent that stimuli do not have the same significance in them. However, nereid species are usually found in well defined habitats, and it may be that habituation rates are innately determined in this animal.

Summary

1. Rates of habituation and response frequencies have been compared in *N. diversicolor, P. dumerilii* and *N. pelagica* to changes in illumination, tactile and mechanical stimuli. In general habituation is rapid to light stimuli and mechanical shocks and slow to tactile stimuli.

2. Worms in tubes are generally more reactive than worms not in tubes.

3. Decerebrate worms respond to the same stimuli as intact ones. They also habituate to them, and similar relationships exist between the response frequencies and rates of habituation to different stimuli in intact and decerebrate worms.

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